

Charixa Lang and *Spinicharixa* gen. nov., cheilostome bryozoans from the Lower Cretaceous

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Synopsis

Seven species of non-ovicellate anascans with pluriserial to loosely multiserial colonies are described from the Barremian–Albian of Europe and Africa. The genus *Charixa* Lang is revised and the following species assigned: *C. vennensis* Lang from the U. Albian Cowstones of Dorset, *C. lhuydi* (Pitt) from the U. Aptian Faringdon Sponge Gravel of Oxfordshire, *C. cryptocauda* sp. nov. from the Albian Mzinene Fm. of Zululand, *C. lindiensis* sp. nov. from the Aptian of Tanzania, and *C.?* sp. from the Barremian Makatini Fm. of Zululand. *Spinicharixa* gen. nov. is introduced for *Charixa*-like species with multiple spine bases. Two species are described: *S. pitti* sp. nov., the type species, probably from the Urganiana Fm. (?Aptian) of Spain, and *S. dimorpha* from the M.–U. Albian Gault Clay of Kent. All previous records of L. Cretaceous cheilostomes are reviewed. Although attaining a wide geographical distribution, cheilostomes remained uncommon, morphologically conservative and of low species diversity until late Albian–early Cenomanian times.

Introduction

An outstanding event in the fossil history of the Bryozoa is the appearance, radiation and dominance achieved by the Cheilostomata during the latter part of the Mesozoic. Aspects of this event have been discussed by several authors (e.g. Cheetham & Cook in Boardman *et al.* 1983; Larwood 1979; Larwood & Taylor 1981; Schopf 1977; Taylor 1981a; Voigt 1981). Comparative morphology provides strong evidence for regarding living cheilostomes as the sister group of living ctenostome bryozoans (Cheetham & Cook in Boardman *et al.* 1983). Fossil ctenostomes have been found as borings (e.g. Pohowsky 1978) and bioimmured casts (e.g. Voigt 1980 and references therein) antedating the oldest cheilostomes, and it is generally thought that a soft-bodied bryozoan resembling the living ctenostome *Arachnidium* was the ancestor of the Cheilostomata (Banta 1975; cf. Dzik 1975 for an alternative view of cheilostome origins). Primitive cheilostomes differ from ctenostomes of the *Arachnidium* type principally in having a hinged operculum to close the orifice, and rigid calcification in parts of the zooid body wall.

Although cheilostomes first appear in the terminal Portlandian Stage of the Jurassic, their major diversification was delayed until the late Cretaceous; rapid morphological evolution and cladogenesis commenced in the late Albian or early Cenomanian and culminated in cheilostome dominance of fossil bryozoan faunas by about the Campanian or Maastrichtian. This spectacular diversification has tended to overshadow the considerable period of slow cheilostome evolution during the 50 million years or so of early Cretaceous time. Little attention has been paid to this 'quiet' phase of cheilostome evolution.

Relatively few species of cheilostomes are known from the L. Cretaceous (see below, p. 198). The principal aim of this paper is to describe a group of species which are especially typical of the L. Cretaceous. They have loosely organized pluriserial or multiserial colonies, and lack ovicells and avicularia. A review of these and other early cheilostomes provides a base from which to assess the later diversification of the group.

Abbreviations of specimen repositories are: British Museum (Natural History)—BMNH; Université Claude Bernard, Lyon—UCBL; South African Museum—SAM; Muséum National

d'Histoire Naturelle, Paris—MNHN. All photographic figures are scanning electron micrographs, using back-scattered electrons, of uncoated specimens, except Figs 25–27 which are of coated latex casts.

Review of Lower Cretaceous cheilostomes

Of the few cheilostomes recorded from the L. Cretaceous, the majority are of late Albian age and most are European or North American occurrences. The literature of L. Cretaceous cheilostomes is reviewed below, chronologically by date of publication.

Mantell (1844) was the first author to describe a probable cheilostome from the L. Cretaceous. *Crisia johnstoniana* Mantell appears to be an encrusting, uniserial cheilostome with caudate zooecia. It was later assigned to *Rhammatopora* Lang by Lang (1915), a genus here regarded as a junior synonym of *Herpetopora* Lang. Mantell's original description gives the geological horizon of *C. johnstoniana* as the Shanklin Sand, while a later description (Mantell 1854) specifies the horizon and locality as the Greensand of Maidstone, presumably Aptian Lower Greensand (Lang 1915). Unfortunately the whereabouts of Mantell's material is unknown and the exact nature of the species is difficult to assess from his stylized illustrations.

In 1853 d'Orbigny described two species of '*Membranipora*' from the French L. Cretaceous. *M. neocomensis* [sic], from the Neocomian of Saint-Sauveur, Yonne, is merely mentioned without description or figure. Voigt (1968) regarded the species as a *nomen nudum*. The poorly-preserved type specimen (d'Orbigny Collection, MNHN No. 5205) is a multiserial colony possibly related to *Wawalia* Dzik. *M. constricta*, from the Aptian of Les Croutes, Yonne, has been restudied by Voigt (1968), who assigned the species to '*Membranipora*' s.l. but noted the lack of correspondence between the putative type specimen (d'Orbigny Collection, MNHN No. 5691) and d'Orbigny's figures (d'Orbigny 1853: pl. 728, figs 9–10). The putative type specimen (see Voigt 1968: pl. 7, fig. 8) and a second specimen in the d'Orbigny Collection have been examined. Both are poorly-preserved multiserial cheilostomes with zooecia that have broad, striated cryptocysts, resembling *Wawalia crenulata* Dzik (see opposite) but without a significant proximal gymnocyst.

Vine (1890a, b) described 5 cheilostome species from the Red Chalk of Hunstanton, most of which is Middle and Upper Albian though some may be Cenomanian (H. G. Owen, personal communication 1985). One of Vine's Red Chalk species was new, *Membranipora gaultina*, and the others were determined as *Membranipora fragilis* (d'Orbigny), *M. elliptica* (?) (Hagenow), *M. obliqua* (?) (d'Orbigny) and *Hippothoa simplex* (d'Orbigny). *M. gaultina* Vine is a uniserial species with strongly caudate zooecia which was later made the type of *Rhammatopora* by original designation by Lang (1915). Thomas & Larwood (1960) characterized *Rhammatopora* by the presence of numerous apertural spine bases, but scanning electron microscope study of the type specimen (BMNH D2062) of *M. gaultina* has failed to confirm these structures and *Rhammatopora* is here regarded as a synonym of *Herpetopora* Lang. The specimen (BMNH D2052) from Hunstanton described by Vine (1890a, b) as *Hippothoa simplex* (d'Orbigny) is undoubtedly conspecific with *Herpetopora gaultina* (Vine) (see Thomas & Larwood 1960: 384). *Membranipora fragilis* (d'Orbigny), *sensu* Vine is represented by an abraded specimen (BMNH D2053) of an encrusting multiserial cheilostome which is too poorly preserved for identification. The single specimen (BMNH D2054) determined as *Membranipora elliptica* (?) (Hagenow) by Vine is another encrusting multiserial cheilostome distinguished by the presence of numerous small polymorphs (probably kenozoecia) which surround and separate the autozooecia. Worn ovicells appear to be present. The whereabouts of Vine's specimen of *Membranipora obliqua* (?) (d'Orbigny) is not known. Vine (1890a) described the specimen as being a dichotomously branched colony with oval, thick-walled zooecia.

Later, in 1892, Vine recorded '*Membranipora gaultina* Vine' and '*Hippothoa*?' (presumably also *Herpetopora gaultina*) from the Gault (Albian) of Barnwell, Cambridge, together with a specimen described as '*Membranipora fragilis* d'Orbigny variety?' from the Gault of Folkestone. The description of this latter species resembles *Spinicharixa dimorpha* sp. nov. (see below, p. 214) except for the apparent presence of ovicells.

Lang (1915) divided Vine's material of *Membranipora gaultina* into two species, *Rhammatopora gaultina* (Vine) for specimens from the Gault Clay, and *R. vinei* Lang for specimens from the Red Chalk in which the mural rim is slightly straighter. The doubtful significance of such a minor feature led Thomas & Larwood (1960) to synonymize the two species. In the same paper Lang described *Charixa vennensis*, a new species belonging to a new monotypic genus, from the Albian Cowstones of Charmouth, Dorset. This species is revised below (p. 201).

Etheridge (1901) described *Lunulites abnormalis* from the L. Cretaceous of Queensland, and in 1902 described *Membranipora? wilsonensis* from the L. Cretaceous of New South Wales, Australia. Both species are in need of redescription and are difficult to assess from Etheridge's original descriptions and figures. *L. abnormalis* forms low cone-shaped colonies with well-defined rows of rectangular zooecia. Although colonies appear to be lunulitiform, assignment of the species to the genus *Lunulites* is questionable; *Lunulites* is unknown in pre-Coniacian deposits. *M.? wilsonensis* has multiserial encrusting colonies with rhombic zooecia. An unusual feature is the presence of a 'spot' (?spine base) on each of the transverse zooecial walls.

Wilbertopora mutabilis from the Albian Fort Worth Formation of Texas was the first L. Cretaceous cheilostome to be described from N. America (Cheetham 1954). The species has since been recorded (Cheetham 1975) from various other formations within the Albian-Cenomanian Washita Group of Texas. *W. mutabilis* is an encrusting anascan with a multiserial arrangement of zooecia, although some colonies have the first few generations of zooecia arranged uniserially. Qualitative and quantitative characters are highly variable. Some colonies, including topotypes, have ovicells, but ovicells are apparently absent in certain 'populations'. Avicularia or avicularian-like polymorphs may be present or absent, and variously shaped. Small orificial spine bases are sometimes present and, more rarely, lateral spine bases.

An additional cheilostome from the Fort Worth Formation was described by Thomas & Larwood (1956) as *Pyrripora texana*. This is a predominantly uniserial species in which the pyriform zooecia have relatively broad caudae. Pairs of tiny apertural spines have been described by Cheetham (1975) in some zooecia of putative conspecific colonies which Cheetham records from several formations in the Washita Group.

A possible junior synonym of *Wilbertopora mutabilis* is *Membranipora? kiowana* described by Scott (1970) from the Kiowa Formation of Kansas, a formation of similar age to those in Texas containing *W. mutabilis* (Cheetham 1975: 552). Dzik (1975), however, refers *M.? kiowana* to his new genus *Wawalia*.

Masse & Walter (1974) briefly describe and figure an un-named fossil from the U. Barremian of Orgon in southern France which they identify tentatively as a cheilostome. The cheilostome affinities of this 'membranipore' are extremely doubtful; the 'zooecia' seem too small (0.16–0.18 mm long) and their arrangement too orderly for an early cheilostome bryozoan.

Larwood's (1975) review of pre-Cenomanian cheilostomes includes mention of three specimens of un-named species from the British Albian which await full description. One of these (BMNH D7477), from the U. Greensand of Warminster, resembles *Wilbertopora mutabilis*. A second (BMNH D31158), from the Haldon Hills, is too poorly preserved for description, while a third (BMNH D38164), from the Cowstones near Charmouth, is described as a unilamellar membraniphorm. Larwood also mentions a pyrriporid cheilostome from the Aptian of Alexander Island, Antarctica, which was described by B. J. Taylor in an unpublished paper presented to the 2nd International Conference of the International Bryozoology Association in Durham during 1971.

Wawalia crenulata was described by Dzik (1975) from the U. Valanginian and L. Hauterivian of Wawal in central Poland. This unusual multiserial species, the second oldest known cheilostome, is characterized by the thickly calcified vertical walls of the zooecia, regular interserial linkage between zooecia via communication pores, a wide cryptocyst which is striated, and irregular pores in the proximal gymnocyst. Specimens of *W. crenulata*, or a closely related species, also occur in the Hauterivian of Lincolnshire and Yorkshire.

The late Aptian Faringdon Sponge Gravel of Faringdon in Oxfordshire is renowned for its rich fauna of cyclostome bryozoans (Canu & Bassler 1926) to which Pitt (1976) added the first record of a cheilostome, '*Membranipora? lhuysdi*'. This species is redescribed below (p. 203) and

assigned to *Charixa*. The introductory remarks in Pitt's paper note the existence of a single specimen of a Neocomian cheilostome from South Africa, as yet undescribed.

Finally, *Pyripopsis portlandensis* Pohowsky, described originally from the Portlandian Stage of the Jurassic (Pohowsky 1973; Taylor 1981*b*), has now been recorded (Ensom 1985) from the Scallop Member of the Purbeck Limestone Formation in Dorset. This extends the range of the species into the Berriasian Stage of the Cretaceous.

Systematic descriptions

Order CHEILOSTOMATA Busk, 1852

Suborder ANASCA Levinsen, 1909

Family ELECTRIDAE Stach, 1937

Non-brooding anascans (and inferred non-brooding anascans) constitute a primitive, paraphyletic group of cheilostomes. Recent representatives of this group are usually divided between the families Electridae and Membraniporidae (e.g. Ryland & Hayward 1977). The former family comprises genera in which the gymnocyst is relatively well developed (e.g. *Electra*, *Pyripora*), the latter those in which it is absent or greatly reduced (e.g. *Membranipora*, *Conopeum*). All the pre-Cenomanian anascans described here have moderately to well developed gymnocysts and are consequently assigned to the Electridae. This is likely to be the more primitive of the two living families. The Membraniporidae are regarded as secondarily reduced (Silén 1942).

Dzik (1975) introduced the Family Wawalidae for *Wawalia* Dzik, *Pyripopsis* Pohowsky, *Charixa* Lang, *Pyripora* d'Orbigny, *Fissuricella* Voigt and possibly *Rhammatopora* Lang. He distinguished the family from the Electridae by the absence of spines. However, occasional zooecia have spines in some colonies of *Pyripora texana* Thomas & Larwood (see Cheetham 1975) and *Charixa lindiensis* sp. nov. (p. 205). This variability raises doubts about the wisdom of using presence or absence of spines as a distinguishing character at this taxonomic level. *Charixa* Lang and *Spinicharixa* gen. nov. are here placed in the Electridae rather than the Wawalidae.

Genus *CHARIXA* Lang, 1915

TYPE SPECIES. *Charixa vennensis* Lang 1915, by original designation.

REVISED DIAGNOSIS. Colonies encrusting, pluriserial with irregularly-arranged, partly contiguous zooecia; distolateral buds usually orientated at a narrow angle to the parent zooecium. Autozooecia ovoidal to pyriform in outline shape; proximal gymnocyst moderately to well developed, sometimes forming a cauda; cryptocyst narrow, steeply sloping, pustulose; spine bases absent or limited to a small distal pair; pore chambers present or presumed to be present. Kenozooecia may occur. Ovicells and avicularia absent.

REMARKS. Based on a revision of the type species, *Charixa* is here used to include primitive, *Electra*-like anascans in which colonies are pluriserial and irregular, the cryptocyst is narrow, steeply sloping, pustulose and has a crenulate margin with the surrounding gymnocyst, and spine bases are absent or limited to a sporadically-developed distal (oral) pair. Colony form resembles *Pyripopsis* Pohowsky but the zooecia of *Charixa* do not have the radially striated cryptocysts and very thick vertical walls typical of *Pyripopsis*. The tendency of *Charixa* colonies to form pluriserial clumps of irregularly arranged zooecia distinguishes the genus from *Pyripora* d'Orbigny, in which the colony is typically uniserial or occasionally narrowly multi-serial and the zooecia are more regularly caudate. However, it should be emphasized that generic concepts in these primitive anascans are made difficult by the paucity of available morphological characters and high levels of phenotypic plasticity among species.

In his original description of *Charixa*, Lang (1915) remarked on the beaded 'termen' (i.e. the opesial margin). As in *Rhammatopora*, Thomas & Larwood (1956) interpreted these beads as

spine bases. However, scanning electron microscope study has failed to reveal the presence of spine bases in Lang's type material, and it is likely that the beads observed by Lang were pustules of the cryptocyst or corrosion pits.

RANGE. Aptian (?Barremian)–Albian. It is unclear whether the genus ranges out of the Lower Cretaceous. A species described as *Pyripora magna* by Larwood (1973), from Campanian (*mucronata* Zone) Chalk of Norfolk, is possibly assignable to *Charixa*.

Charixa vennensis Lang 1915

Figs 1–3

1915 *Charixa vennensis* Lang: 501; pl. XVII, figs 5–6.

HOLOTYPE. BMNH D22950. Cowstones, Upper Greensand, Upper Albian (*inflatum* Zone, *varicosum* Subzone). Black Ven, Charmouth, Dorset, England.

PARATYPES. A large suite of specimens was apparently used by Lang when describing *C. vennensis*, and these are labelled as paratypes in the BMNH collections. They consist of the following: D20483 (2 specimens)–D20487 'Albian, zone of *Hoplites interruptus*, Gault, Bed 3, Section d, Black Ven, Charmouth'; D22931–41, D22946–49, D22951–85 'Albian, zone of *Mortonicerias rostratum*, Cowstones, Black Ven, Charmouth'; D23021–24 'Albian, Gault, zone of *Hysterocheras varicosum*, Dunton Green, N. of Sevenoaks, Kent, F. Möckler Colln'. Of these paratypes, only D22948–49 and D22951–52 can be positively determined as *C. vennensis*. The remainder are too heavily corroded for identification, reveal only the featureless underside of the colony, or belong to different species (the Dunton Green specimens are *Herpetopora gaultina* (Vine) and *Spinicharixa dimorpha* sp. nov.).

DESCRIPTION. Colonies are encrusting, uniserial or more typically pluriserial with the zoecia arranged in irregular fans and clusters (Figs 1a, 2). Budding is distal and distolateral, the latter usually at a small angle ($<60^\circ$) to the parent zoecium but occasionally at right angles. Depending on the exact angle of distolateral budding, distolaterally budded zoecia may be separated from or partly contiguous with distally budded ones arising from the same parent zoecium.

Autozoecia are generally pyriform and have well-developed proximal gymnocysts forming caudae less than half the total length of the zoecium. However, in crowded areas the proximal

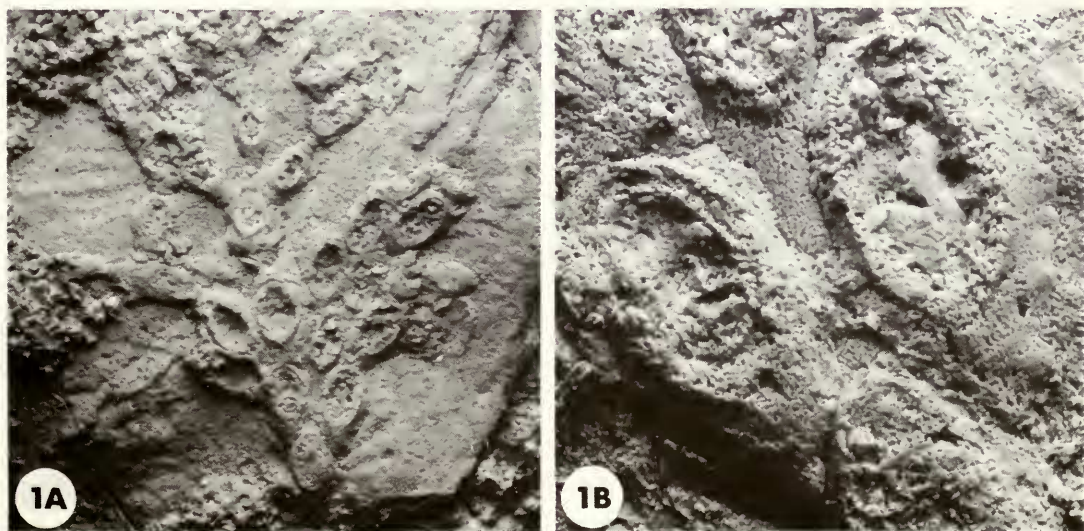


Fig. 1 *Charixa vennensis* Lang. BMNH D22950. Holotype. Cowstones (Albian); Black Ven, Dorset. 1A, fan-like colony-form, $\times 28$; 1B, poorly-preserved zoecia with pustulose cryptocysts, $\times 140$.

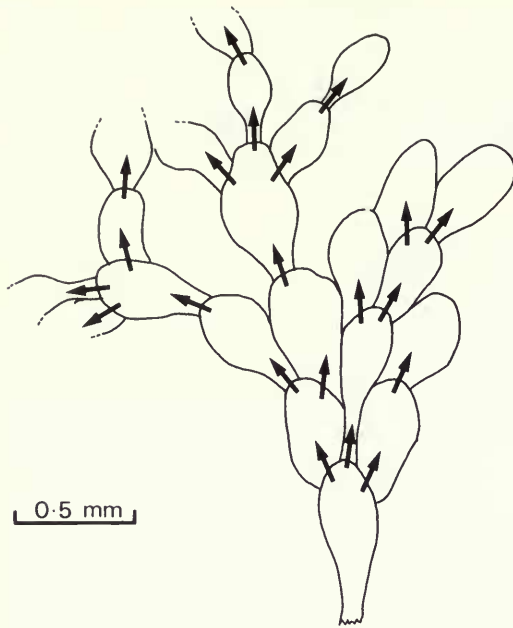


Fig. 2 *Charixa vennensis* Lang. BMNH D22950. Holotype. Outline diagram of zoecia to show budding pattern. Arrows indicate directions of budding. Note the abnormally small zoecia budded at the distal ends of the branches on the left.

gymnocyist is reduced and the autozooeceum is more elliptical in shape. Autozooeceal size varies considerably within colonies (Fig. 1a; Table 1, p. 219), length averaging 0.51 mm and width 0.24 mm in the holotype. The occurrence of small autozoecia budded from distinctly larger autozoecia in the holotype (Figs 1a, 3a) led Lang (1915) to suggest rejuvenescence of growth. Opesiae are oval, and almost twice as long ($\bar{x} = 0.24$ mm) as wide ($\bar{x} = 0.14$ mm). The cryptocyst is steeply sloping, pustulose, and has a crenulate margin with the surrounding gymnocyist (Fig. 1b). There are no indications of spine bases (cf. Thomas & Larwood 1956). Some autozoecia have regenerations and others are occluded by closure plates which are flat or slightly depressed, and bear crescent-shaped depressions made by the opercular sclerites (Fig. 3b). Pore chambers are not visible in the holotype nor in those paratype specimens which are unequivocal.



Fig. 3 *Charixa vennensis* Lang. BMNH D22950. Holotype. Cowstones (Albian); Black Ven, Dorset. 3A, autozooeceum with closure plate budding small autozoecia distally and distolaterally, $\times 90$; 3B, damaged closure plate with an opercular impression, $\times 230$.

cally conspecific with it, but they can be seen in possibly conspecific colonies in which only the undersides of the zooecia are visible.

Kenozoocia may occur filling irregular spaces between autozoocia. They are polygonal in outline and have slightly concave edges. The frontal surface seems to be completely calcified, i.e. opesiae are lacking.

The ancestrula has not been observed. Avicularia and ovicells are unknown.

REMARKS. Unfortunately, none of the available specimens of *C. vennensis* is well preserved. Adherent sand grains obscure zooecial details and on removal leave pits in the calcification. These corrosion pits, emphasized by staining with watercolour paint, were possibly misinterpreted as spine bases by Thomas & Larwood (1956).

Colonies encrust fragments of mollusc (probably bivalve) shells.

DISTRIBUTION. U. Albian (*inflatum* Zone, *varicosum* Subzone), known only from Black Ven, Charmouth.

Lang (1915) records *C. vennensis* from two stratigraphical levels on Black Ven. These he gives as Bed 3 in the *Hoplites interruptus* Zone, and the Cowstones in the lower part of the *Mortoniaceras rostratum* Zone. The former horizon is probably the clayey silt regarded as M. Albian *dentatus* Zone by Wilson *et al.* (1958: 141). However, none of the specimens from this level are sufficiently well preserved to be confirmed as *C. vennensis*. Lang's second horizon probably corresponds with the 'Lower Sands with Cowstones' of Wilson *et al.* (1958) and is of the U. Albian *inflatum* Zone, *varicosum* Subzone (H. G. Owen, personal communication 1985).

Charixa lhuydi (Pitt 1976)

Figs 4–5

1976 '*Membranipora*' *lhuydi* Pitt: 65; pl. 1, figs A–D.

HOLOTYPE. BMNH D52494. Faringdon Sponge Gravel, U. Aptian (*nutfieldensis* Zone). Little Coxwell Pit, Faringdon, Oxfordshire. L. J. Pitt Colln.

PARATYPE. BMNH D52495. Same details as holotype.

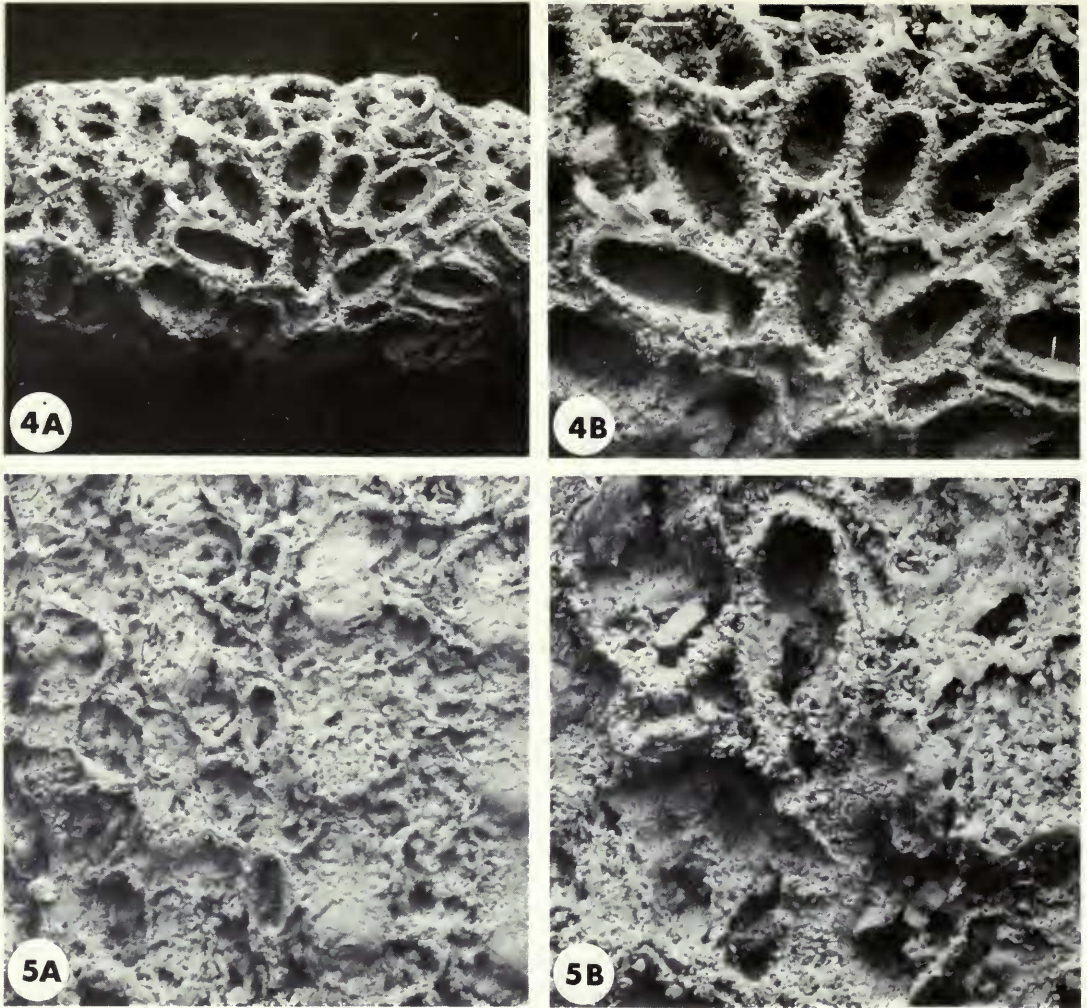
ADDITIONAL MATERIAL. BMNH D54190–200, Faringdon Sponge Gravel, locality unknown, G. J. Hinde Colln. BMNH D55067, as holotype, A. G. Davis Colln. BMNH D55068, as holotype, G. F. Elliott Colln.

DESCRIPTION. Colonies are encrusting and comprise irregular pluriserial patches of zooecia (Fig. 4a) which sometimes show multilamellar overgrowth. Zooecial orientations and budding positions are difficult to ascertain in the poorly-preserved material which is available. However, in one specimen (BMNH D54191) a line of caudate autozoocia appears to bud distolateral non-caudate autozoocia of the type more typical for the species (Fig. 5).

Autozoocia are usually elliptical in outline (Fig. 4b) and have a slight proximal gymnocyst. Rarely, autozoocia are pyriform (Fig. 5b) and have a caudate proximal gymnocyst about half the length of the zooecium. In the holotype, autozoocial length averages 0.44 mm and width 0.33 mm. Opesiae are elongate elliptical and occupy most of the frontal surface of the majority of autozoocia. Cryptocysts are usually obscured by calcite cement but appear to be steeply sloping and seem to be pustulose. Unequivocal closures and regenerations have not been observed. Communication pores are present as windows in vertical walls (see Pitt 1976: pl. 1, fig. D), but the expected presence of pore chambers has not been confirmed in this poorly-preserved material.

Some of the irregular spaces between autozoocia appear to be occupied by kenozoocia with extensive opesiae. These were perhaps misidentified as broken ovicells by Pitt (1976). Avicularia and unequivocal ovicells are absent. The ancestrula is unknown.

REMARKS. Since Pitt's (1976) original description of this species several additional specimens have become available. Unfortunately these share the poor preservation of the holotype and paratype. A considerable growth of calcite cement obscures surface details, and several of the



Figs 4-5 *Charixa lhuydi* (Pitt). Faringdon Sponge Gravel (Aptian). Fig. 4, BMNH D55068, Little Coxwell Pit, Faringdon; 4A, colony encrusting a branch fragment of *Meliceritites*, $\times 37$; 4B, autozoecia with oval opesia, $\times 65$. Fig. 5, BMNH D54191, locality unknown; 5A, line of three caudate autozoecia (centre) growing in the furrow of an echinoid spine, $\times 37$; 5B, caudate autozoecium, $\times 112$.

colonies are abraded. However, the finding of a colony (BMNH D54191) with a line of caudate autozoecia (Fig. 5) suggests assignment of the species to *Charixa*. These caudate autozoecia follow a furrow in the echinoid spine encrusted by the colony. Their distolateral buds appear to be non-caudate autozoecia of the kind which predominate in *C. lhuydi* colonies. By comparison with *Spinicharixa dimorpha* (p. 214), it is thought that the caudate autozoecia represent an initial runner-like growth across the substratum.

All known specimens except one encrust spines of regular echinoids. Colonies often occupy the entire circumference of the spine and are usually absent from the collar region. Spines of Recent echinoids are frequently fouled by epizoans (including bryozoans) while the echinoid is still alive (Mortensen 1928: 27), but remain free of encrusters on the collars of the spines where muscles attaching the spine to its base are situated. It appears possible that *C. lhuydi* was a life

associate of echinoids, although the single colony (BMNH D55068) of *C. lhuydi* encrusting an erect branch of the cyclostome *Meliceritites* shows that the association was not entirely obligatory for the bryozoan.

DISTRIBUTION. U. Aptian (*nutfieldensis* Zone), Faringdon Sponge Gravel of Faringdon, Oxfordshire, England.

Charixa cryptocauda sp. nov.

Figs 6–7

HOLOTYPE. SAM PCZ7306. Mzinene Formation, Albian, subdivision IV or V of Kennedy & Klinger (1975). Stream bed and bank exposures in eastern limb of broad meander, ENE of sisal factory, north of Hluhluwe, Zululand, South Africa. Locality 51 of Kennedy & Klinger (1975). W. J. Kennedy Colln.

PARATYPE. SAM PCZ7307. Same details as holotype.

NAME. In reference to the cauda becoming hidden by later zooecial buds.

DESCRIPTION. Colonies are encrusting with uniserial chains of zooecia (Fig. 6a) or pluriserial sheets of irregularly-arranged zooecia (Fig. 7a). Initial budding appears to have been predominantly distal, giving uniserial chains, but later distolateral and occasionally proximolateral budding produced zooecia which infilled the substrate between the uniserial chains and overgrew the caudae of earlier zooecia.

Autozooecia are elliptical to pyriform in outline shape, depending upon the length of the proximal gymnocyst which can be short or can form a distinct cauda up to half the total length of the zooecium. Average autozooecial length in the holotype is 0.53 mm, width 0.24 mm. Opesiae are usually about twice as long as wide, and roughly elliptical but with a tendency to be square-ended. The cryptocyst is narrow, steeply sloping, pustulose, and has a crenulate border with the surrounding gymnocyst. Many zooecia have large distolateral and proximolateral communication pores visible as windows in the vertical walls. Distal pore chambers may be well-developed (Fig. 7b). Regenerations occur rarely and closure plates are seldom found. However, an autozooecium in the paratype has a closure plate which is slightly depressed below the level of the mural rim, flat-surfaced, and incompletely calcified leaving an elongate median perforation (Fig. 6b). The closure plate bears a semicircular impression of the operculum which was evidently about 0.10 mm wide.

Kenozoecia occur abundantly in the holotype (Fig. 7c). They are irregular, mainly triangular or diamond-shaped, and have slightly concave sides. Kenozoecial cryptocysts resemble those of autozooecia but the opesiae are smaller and less regular. Bud fusion appears to occur in the formation of at least some of the kenozoecia (Fig. 7d).

Ovicells and avicularia have not been observed. The ancestrula is unknown.

DISCUSSION. *C. cryptocauda* is distinguished from previously described species of *Charixa* and similar genera by the unusual overgrowth of the caudae of early budded autozooecia by later autozooecia, particularly kenozoecia. The result is reminiscent of the Recent hiantoporidae *Dactylostega prima* Hayward & Cook, 1983 in which autozooecial boundaries become obscured by the budding of interzooecial avicularia and ?kenozooids onto the colony surface.

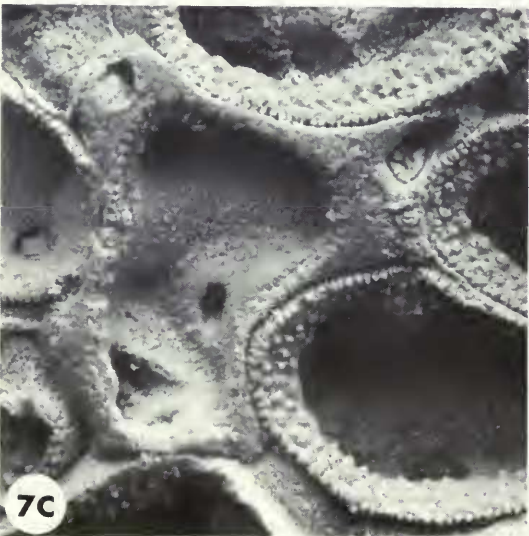
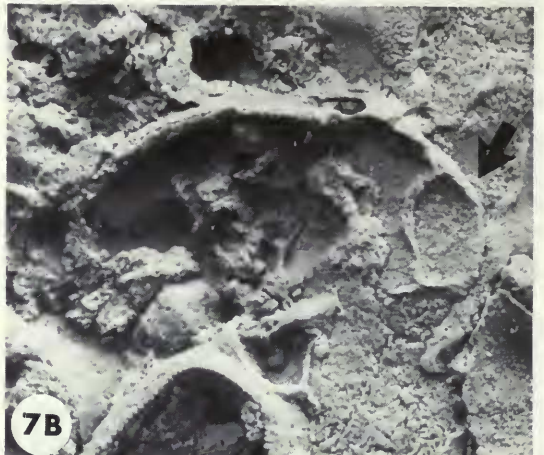
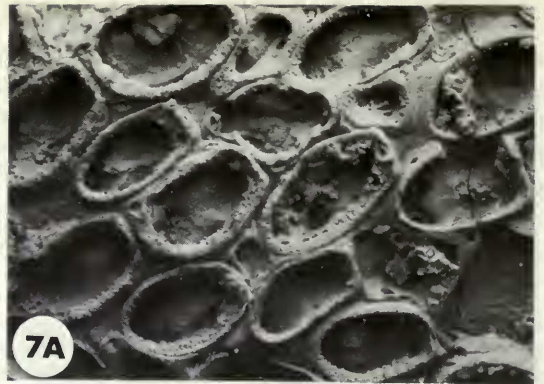
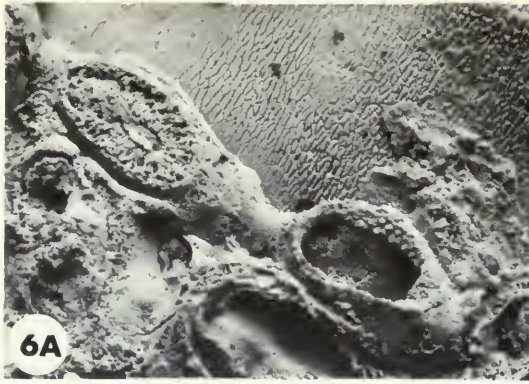
The holotype colony encrusts the epifaunal gastropod *Eriptycha* sp., whereas the paratype colony encrusts an oyster together with serpulids and foraminifers.

DISTRIBUTION. Albian (subdivision IV or V of Kennedy & Klinger, 1975), Mzinene Fm., of Hluhluwe, Zululand, South Africa.

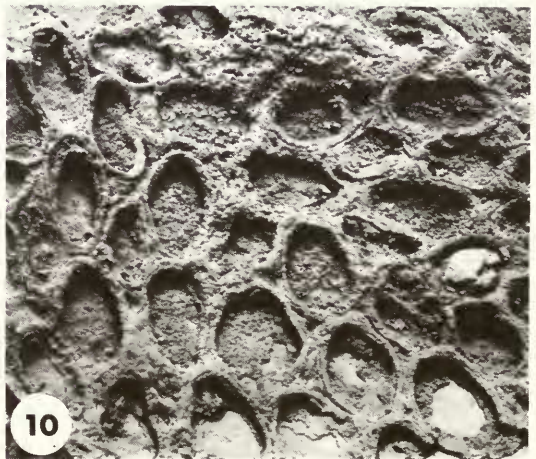
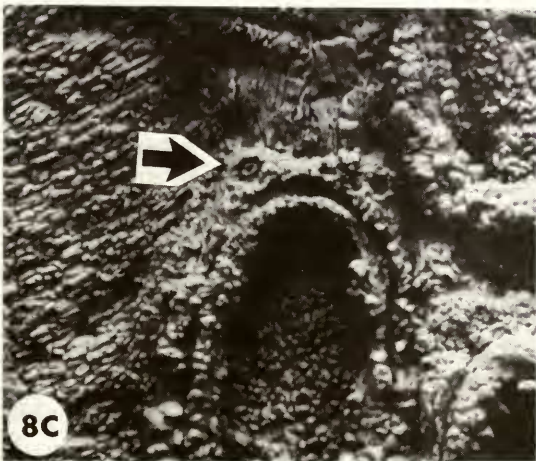
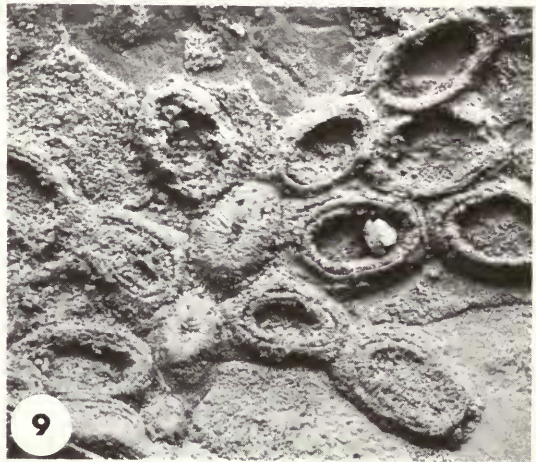
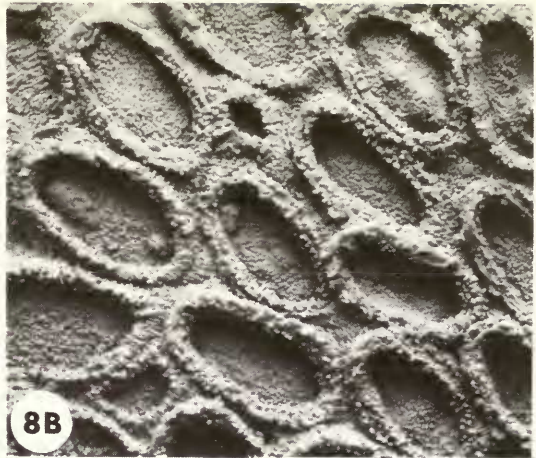
Charixa lindiensis sp. nov.

Figs 8–10

HOLOTYPE. BMNH D55025a. Aptian. 1–1.5 miles from Utimbe on the Libobe road, Lindi, Mtwara Province, Tanzania. G. M. Stockley Colln.



Figs 6-7 *Charixa cryptocauda* sp. nov. Mzinene Formation (Albian); N. of Hluhluwe, Zululand. Fig. 6, SAM-PCZ 7307, paratype; 6A, caudate autozoocia, $\times 93$; 6B, perforated closure plate of autozoecium with opercular scar, $\times 130$. Fig. 7, SAM-PCZ 7306, holotype; 7A, crowded autozoocia and kenozoocia, $\times 53$; 7B, abraded autozoecium showing large distal pore chamber (arrow), $\times 150$; 7C, kenozoecium filling the area between autozoocial opesia, $\times 200$; 7D, incipient kenozoecium arising as two or three separate buds onto the proximal gymnocyst of an autozoecium, $\times 190$.



Figs 8–10 *Charixa lindiensis* sp. nov. Aptian; Lindi, Mtwara Province, Tanzania. Fig. 8, BMNH D55025a, holotype; 8A, lobate colony-form, $\times 24$; 8B, autozooezia and a diamond-shaped kenozoecium, $\times 83$; 8C, pair of distal spine bases (arrow), $\times 240$. Fig. 9, BMNH D55026b, paratype, astogenetically early autozooezia with closure plates and regeneration rims, $\times 67$. Fig. 10, BMNH D55026a, paratype, oblique view of crowded, worn autozooezia, $\times 46$.

PARATYPES. BMNH D55025b, encrusting the same substrate as the holotype. BMNH D55026a, b, Aptian, Utimbe, Lindi, Mtwara Province, Tanzania. G. M. Stockley Colln.

NAME. From the Tanzanian district of Lindi.

DESCRIPTION. Colonies are encrusting and pluriserial with zooecia sometimes arranged in fan-like expansions (Fig. 8a) or irregular clumps (Fig. 10), although early zooecia may have a looser, more uniserial configuration (Fig. 9).

Autozooecia are elliptical to slightly pyriform in shape (Figs 8b, 9). The proximal gymnocyst is of slight to moderate length, not exceeding one quarter of total zooecial length. Autozooecia are relatively small, averaging 0.41 mm long by 0.20 mm wide in the holotype (Table 1, p. 219). Opesiae are elongate ellipsoidal, about twice as long as wide, sometimes slightly square-ended. Rarely autozooecia have a pair of distal spine bases (Fig. 8c). These are small, oval, and have a concentric inner ring (as in *Spinicharixa* spp. and *Callopora lineata*). A steeply sloping cryptocyst appears to be present but details are obscured by surface growth of cement crystals. Pore chambers have not been observed. Several autozooecia have a single, rarely two, regenerations. Closure plates occur in a few early autozooecia of specimen D55026b (Fig. 9). They are convex and weathered to reveal a radiating microstructure and a narrow uncalcified median area. A pair of slit-like opercular sclerite impressions on the closure plate indicates an operculum width of about 0.04 mm.

The holotype has a kenozoecium (Fig. 8b) which is elongate diamond-shaped with a broad gymnocyst surrounding the opesia. Avicularia and ovicells are absent. The ancestrula has not been observed.

REMARKS. *C. lindiensis* is distinguished from other species of *Charixa* by the consistently small size of the zooecia, and the very occasional development of a pair of distal spine bases. In the sporadic occurrence of distal spine bases *C. lindiensis* resembles the uniserial Albian species *Pyripora texana* (see Cheetham 1975), although it is not clear whether the spine bases in *P. texana* also have a concentric ring structure.

Each colony encrusts either the exterior or the interior surface of an oyster.

DISTRIBUTION. Aptian of Utimbe, Lindi Province, Tanzania.

Colonies of *C. lindiensis* were found among a sample of oysters in the mollusc collections of the BMNH. These oysters were collected from the area of Utimbe in about 1930 by G. M. Stockley, then employed by the Geological Survey of Tanganyika and later to become Director. The Utimbe area is mapped only as undifferentiated Cretaceous (1:500,000 scale map produced by BP Shell Petroleum Development Co., Tanganyika, and dated 1960), and the oysters themselves are not age diagnostic (N. J. Morris, personal communication 1985). However, the correspondence files of the BMNH contain a letter dated 23 June 1930 from L. R. Cox to G. M. Stockley concerning the Utimbe specimens. The letter notes the existence of associated fragments of the Aptian ammonite *Chelonicerias* which were determined by L. F. Spath.

Charixa? sp.

Fig. 11

MATERIAL. BMNH D55062. Bed 18, Makatini Fm., Barremian. Locality 170 of Kennedy & Klinger (1975), 2 km NW of the store on north side of stream, Mlambongwenya Spruit, Northern Zululand, South Africa. W. J. Kennedy Colln.

DESCRIPTION. An encrusting colony which is partly uniserial but mainly pluriserial with zooecia arranged irregularly. Distolateral buds are usually orientated at a small angle to the axis of the parental zooecium.

Autozooecia are large, averaging about 0.72 mm long by 0.34 mm wide, and elliptical to pyriform in shape with variable development of the proximal gymnocyst (Fig. 11a). Opesia are elliptical and generally twice as long as wide. No cryptocyst is visible; radial fissures in the mural rim seem to represent the weathered microstructural fabric of the gymnocyst (Fig. 11a-b). Some autozooecia have closure plates (Fig. 11b) but opercular scars are not evident.

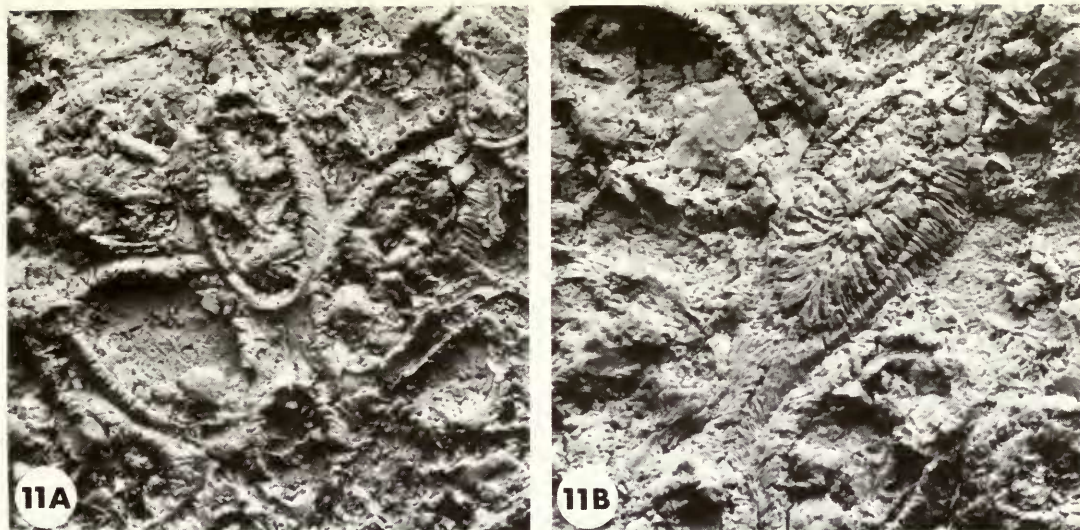


Fig. 11 *Charixa?* sp. BMNH D55062, Makatini Formation (Barremian); Mlambongwenya Spruit, Zululand; 11A, worn autozooeceum with open opesia, $\times 64$; 11B, worn autozooeceum with closure plate, $\times 73$.

A few irregular, space-filling kenozooeceum with wide opesia occur. Ovicells and avicularia have not been observed.

REMARKS. Colony-form and zooecial shape in this Barremian species are typical of *Charixa* but a cryptocyst is apparently lacking. Therefore assignment to *Charixa* is questionable. Full description of the species must await the availability of more material.

Genus *SPINICHARIXA* gen. nov.

TYPE SPECIES. *Spinicharixa pittii* sp. nov.

DIAGNOSIS. Colonies encrusting, pluriserial or multiserial with quite regularly arranged zooecia. Autozooeceum ovoidal to pyriform in outline shape; proximal gymnocyst slightly to well developed, sometimes forming a cauda; cryptocyst narrow, steeply sloping, pustulose; spine bases numerous, each with an inner concentric ring, indenting the margin of the cryptocyst; pore chambers present in ontogenetically young zooecia but apparently resorbed in many older zooecia. Ancestrula budding a distal zooecium and possibly additional zooecia proximally and laterally. Kenozooeceum may occur. Ovicells and avicularia absent.

NAME. Like *Charixa* but spinose.

REMARKS. *Spinicharixa* is introduced for primitive, non-ovicellate anascans resembling *Charixa* but possessing numerous spine bases ringing the opesia of the autozooeceum. Zooecial arrangement tends to be more regular in *Spinicharixa* than *Charixa*. In *S. pittii* interzooecial gaps, common in species of *Charixa*, are seldom found, and parts of the essentially multiserial colonies have a regular quincuncial arrangement of subrhomboidal zooecia. *S. dimorpha*, however, is more *Charixa*-like in having an essentially pluriserial colony-form with some interzooecial gaps.

RANGE. ?Aptian–Albian.

Spinicharixa pitti sp. nov.

Figs 12–18

HOLOTYPE. UCBL EM30401b. Probably Urgoniana Formation, ?Aptian. Utrillas, Spain, Coquand Colln 1867.

PARATYPES. UCBL EM30401a, c, d, e, colonies encrusting same substrate as holotype. EM30402, details as for holotype. EM30409 (several groups of zooecia which may represent many colonies or a single fragmented colony), details as for holotype but Verneuil Colln.

NAME. For Leslie J. Pitt, in recognition of his many years of research on Aptian bryozoans.

DESCRIPTION. Colonies are encrusting, with the first 4 or 5 generations of zooecia arranged uniserially (Fig. 14) before rapidly expanding into a multiserial sheet. Multiserial parts of colonies have a compact, near quincuncial arrangement of zooecia (Fig. 12) with little inter-zooecial space. However, linear series of more caudate zooecia (Fig. 13a) may sometimes be distinguished within the multiserial sheet suggesting that growth pattern may perhaps have resembled that of *S. dimorpha* which is described below (p. 215). Well-preserved growing edges have not been observed.

Autozooecia are elliptical to rounded rhomboidal in shape, averaging 0.41 mm long by 0.25 mm wide. Opesiae are extensive and elliptical in shape, sometimes slightly square-ended. The proximal gymnocyst is usually short but is fairly well developed in a few lineal series of zooecia. The cryptocyst is moderately broad, steeply sloping and pustulose (Fig. 15c) with a crenulate margin with the surrounding gymnocyst. Pustules are arranged in 4 or 5 ill-defined alternating rows, become sparser basally, and are lacking from the distal end of the zooecium. Each autozooecium has 4–7 spine bases, generally paired, which are situated within the gymnocyst but indent the cryptocyst (Fig. 17). The spine bases (Fig. 18) are circular or elliptical (elongated parallel to the edge of the opesia) and variable in diameter (\bar{x} = 0.02 mm; observed range = 0.01–0.04 mm). The edge of the spine base is slightly raised and an inner concentric ring is situated within the conical central depression. Large pore chambers may occur in distal and distolateral positions. Several autozooecia, possibly all occluded by closure plates, have

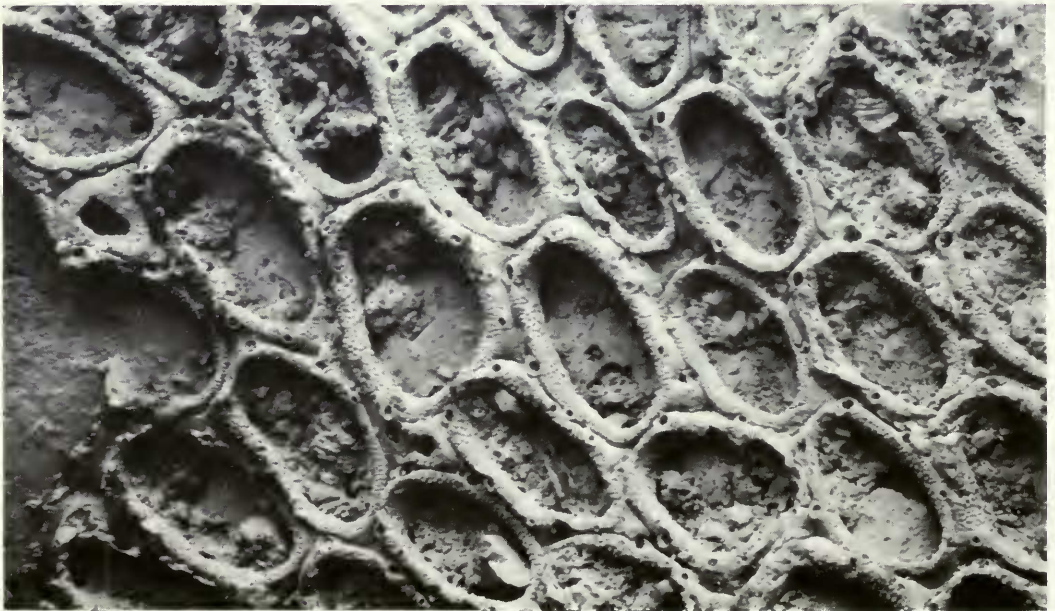
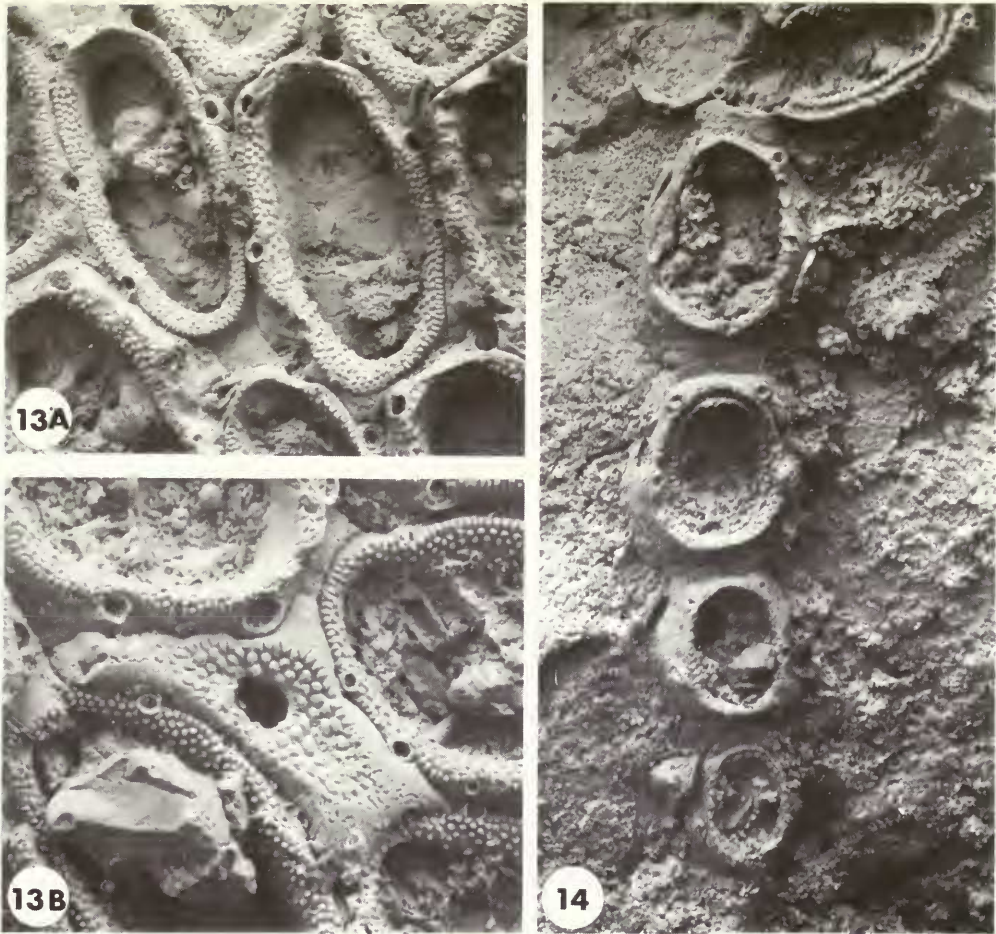


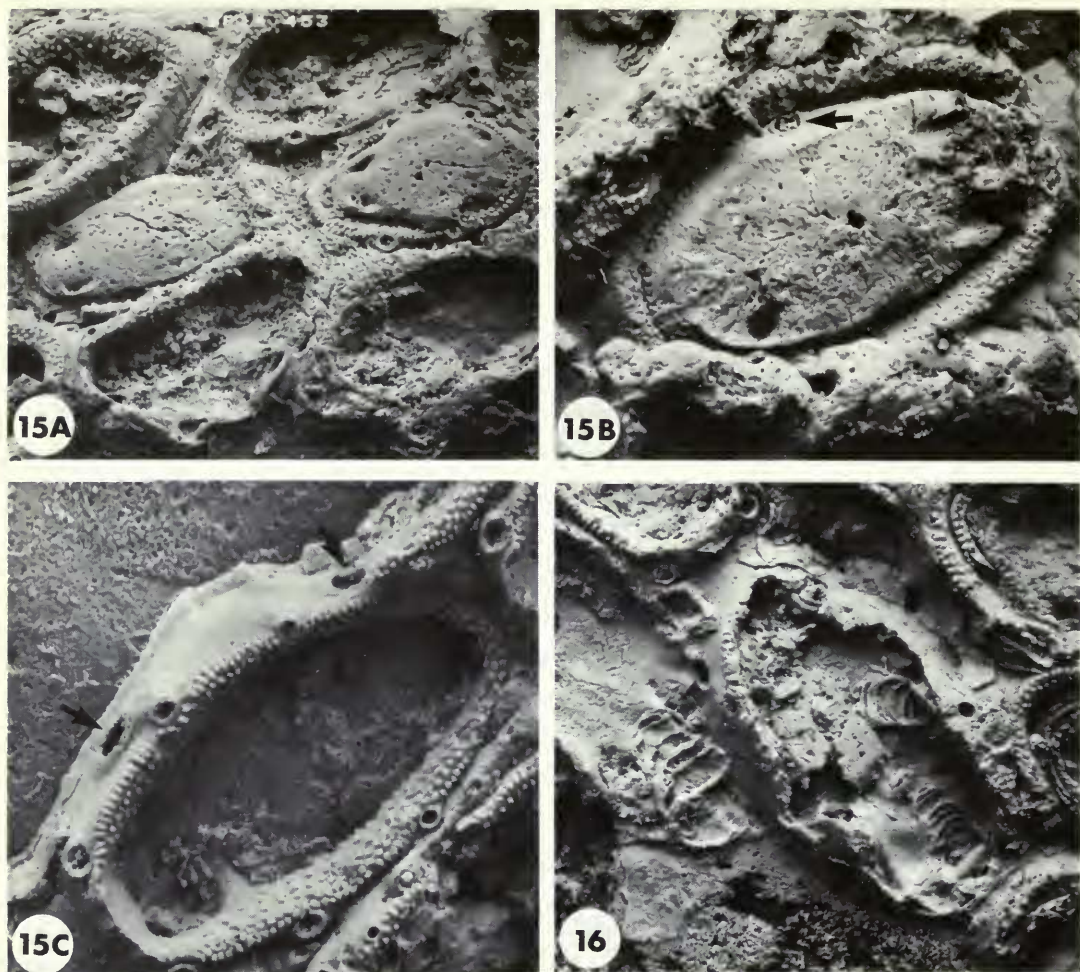
Fig. 12 *Spinicharixa pitti* gen. et sp. nov. UCBL EM30401b, holotype; probably Urgoniana Formation (?Aptian); Utrillas, Spain; slightly oblique view of colony surface, $\times 65$.



Figs 13–14 *Spinicharixa pitti* gen. et sp. nov.; probably Urganiana Formation (?Aptian); Utrillas, Spain. Fig. 13, UCBL EM30401b, **holotype**; 13A, autozoecia showing spine bases and pustulose cryptocysts, $\times 110$; 13B, kenozoecium, $\times 134$. Fig. 14, UCBL EM30401d, paratype; ancestrula and first three generations of budded autozoecia arranged uniserially, $\times 143$.

unusual elongated pore chambers which are partitioned transversely by up to 10 arcuate walls convex towards the interior of the zooecium (Fig. 16). Communication pore windows in free exterior walls are large and elliptical. Interserial communication between zooecia is suggested by the presence in some zooecia of proximolateral pores as well as distal and distolateral pores (Fig. 15c). Regeneration rims may occur (Fig. 14). Closure plates are of two types: in one the plate is convex and joins the crenulate edge of the gymnocyst; in the second the plate is surrounded by a deep marginal furrow and has a sloping edge (sometimes penetrated by spine bases located inwards of the usual spine bases) and a flat top (Fig. 15a, b). The first type is interpreted as a simple closure, whereas the second may be a closure plate formed by a zooid with a regeneration. Closure plates of the latter type may have a system of irregular radial surface fissures, and an opercular scar with sclerite impressions 0.07–0.08 mm apart.

The ancestrula and early buds (Fig. 14) are well preserved in paratype colony UCBL EM30401d but less well preserved in the holotype colony. The ancestrula is small, elliptical in shape, and broad in comparison with later zooids, about 0.16 mm long by 0.14 mm wide. Swellings of the gymnocyst, partly obscured by sediment, may represent one or a pair of spine



Figs 15–16 *Spinicharixa pittii* gen. et sp. nov.; probably Urganiana Formation (?Aptian); Utrillas, Spain. Fig. 15, UCBL EM30401b, **holotype**; 15A, two autozooezia with closure plates, $\times 90$; 15B, autozooezium with closure plate incorporating a spine base (arrow), $\times 224$; 15C, autozooezium with windows (arrows) of pore chambers in free exterior wall, $\times 148$. Fig. 16, UCBL EM30402, paratype, broken pore chambers partitioned by arcuate plates, $\times 120$.

bases situated about mid-length. There is a single distally-budded periancestrular autozooezium with 4 spine bases. The first 4 or 5 generations of zooezia are arranged uniserially and show a progressive increase in size.

Kenozooezia (Figs 13b, 17) occur as space-filling structures which are smaller than autozooezia, and generally have 4 concave sides. The cryptocyst is broad, flat, has coarse pustules and a crenulate margin with the gymnocyst. Opesia are small and elliptical.

Ovicells and avicularia are not present.

REMARKS. *Spinicharixa pittii* is distinguished from previously described non-ovicellate anascans by the abundant spine bases with a distinctive concentric structure, and from *S. dimorpha* by the lack of dimorphism of autozooezia.

There is a slight resemblance between *S. pittii* and *Distelopora bipilata* described by Lang (1915) from the Chalk Marl of Cambridge. In this Cenomanian species, however, the spine bases appear not to have an inner ring, and the cryptocyst seems to overlap the gymnocyst. All

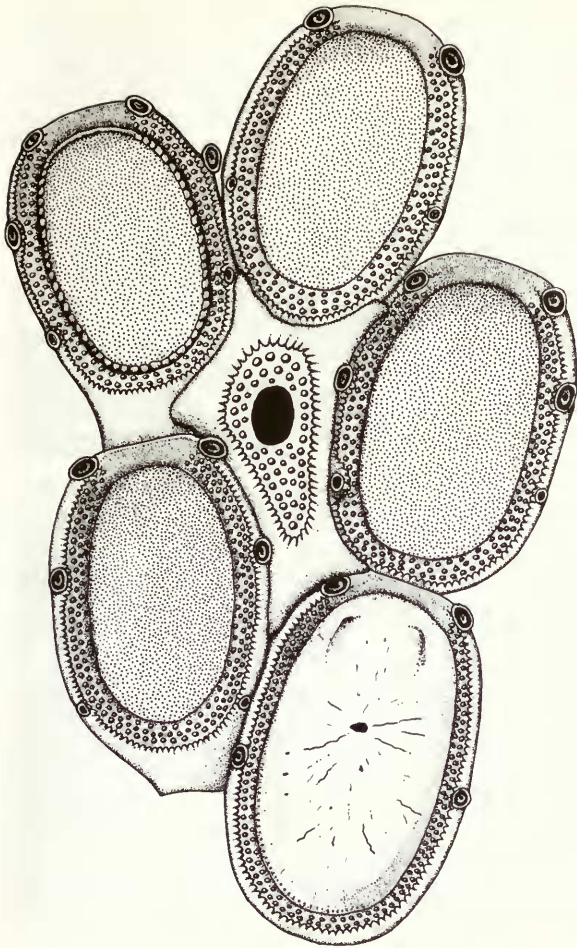


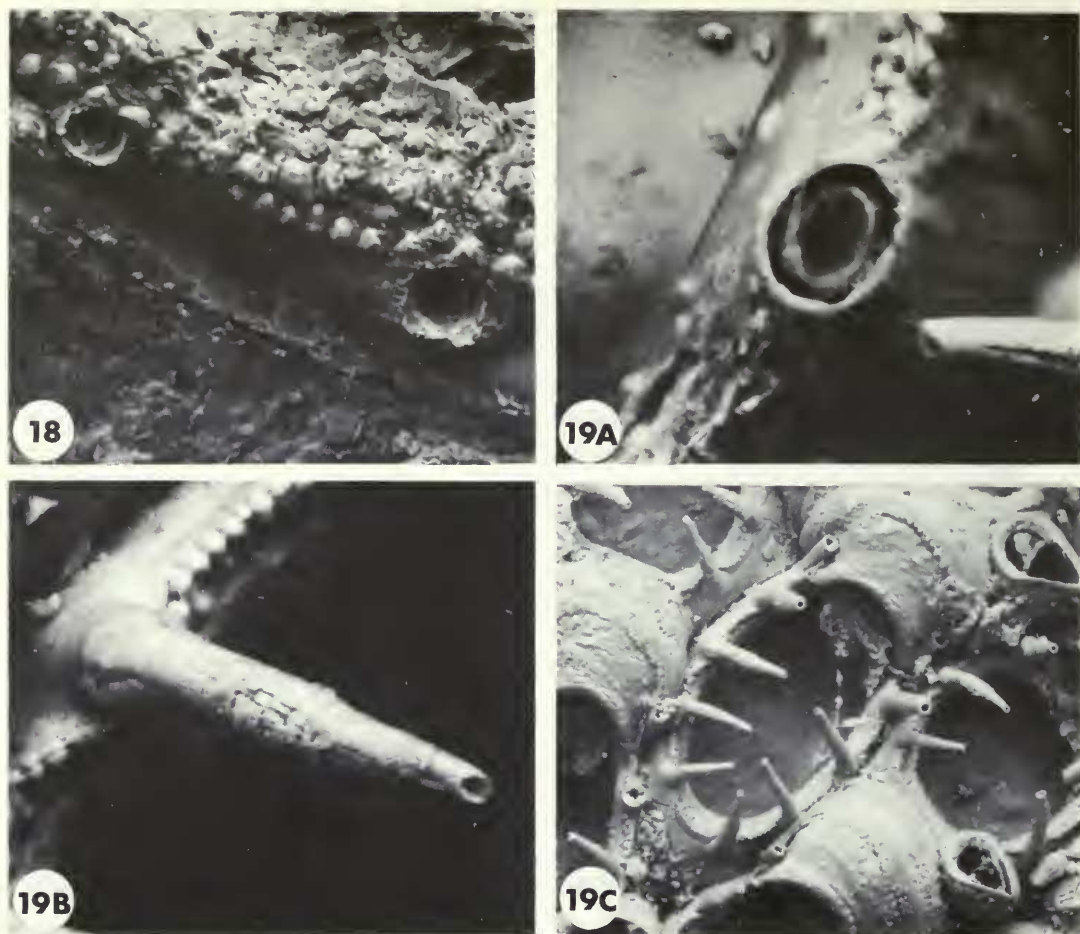
Fig. 17 *Spinicharixa pitti* gen. et sp. nov. Composite drawing of 5 autozooezia surrounding a kenozooezium. The autozooezium bottom right has a closure plate of the type formed after regeneration; the autozooezium top left has a regeneration rim.

specimens of *D. bipilata* consist of small colonies and it is possible that ovicells and avicularia developed during later stages of colony growth.

The spine bases of *S. pitti* strongly resemble those of the living *Callopora lineata*. In both species the spine base has a crater-like shape with an inner concentric ring (Figs 18, 19a). The intact spines of *C. lineata* are hollow and pointed, and overarch the frontal membrane of the zooid (Figs 19b, c). A similar morphology is envisaged for *S. pitti*, although the high variability in spine base diameter could indicate more variation in spine size than in *C. lineata*. The basal area of the spine seems to represent a point of weakness from which the spines may have become detached accidentally or perhaps shed during the ontogeny of the zooid.

Colonies of *S. pitti* encrust the epifaunal gastropod *Paraglauconia lujani* (de Verneuil & Collomb). Most occur on apical whorls but colony UCBL EM30409f is situated on the inner lip, an area which would have been covered by mantle tissue during the life of the gastropod, implying that the gastropod became encrusted *post mortem*.

DISTRIBUTION. ?Aptian. There are uncertainties about the exact stratigraphical level from which these museum specimens were collected. A Barremian–Cenomanian sequence exposed in the region of Utrillas has been described by Aguilar *et al.* (1971). Cassioid gastropods like those encrusted by *S. pitti* appear to be present in the Urgoniana Formation which is partly Barremian but mostly Aptian. The same gastropod species also occurs in the L. Aptian (*forbesi* Zone) Punfield Marine Bed of Dorset (Cleevely *et al.* 1984).



Figs 18–19 Spines and spine bases in *Spinicharixa* and *Callopora*. Fig. 18, *Spinicharixa pittii* gen. et sp. nov.; UCBL EM30402, paratype; probably Urganiana Formation; Utrillas, Spain; two spine bases with inner concentric rings, $\times 530$. Fig. 19, *Callopora lineata* (Linné), BMNH Zoology Department 1911.10.1.513a; Recent; Durham Coast; 19A, spine base with inner concentric ring, $\times 740$; 19B, intact spine, $\times 610$; 19C, ovicelled autozooeceum with spines over-arching the opesia, $\times 125$.

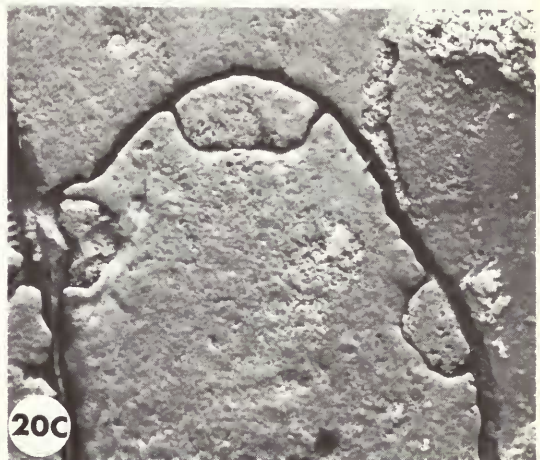
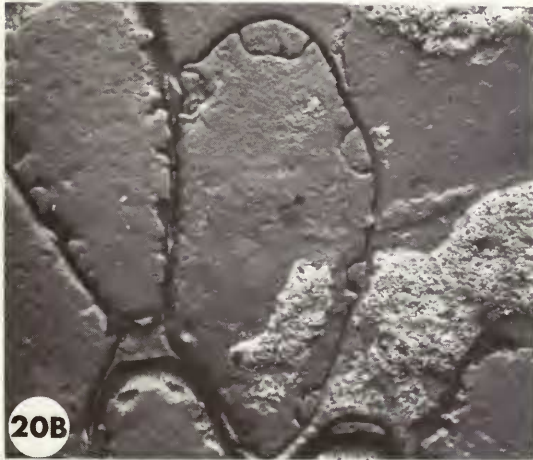
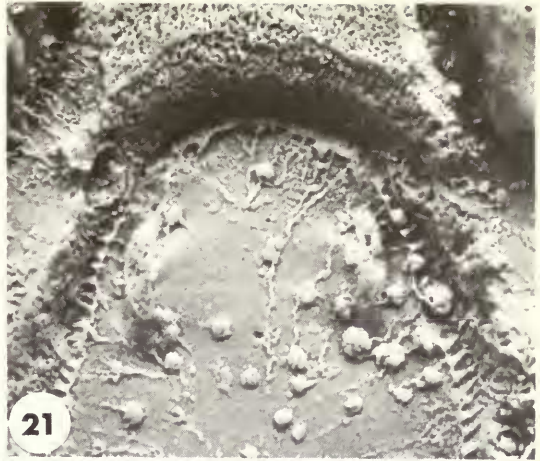
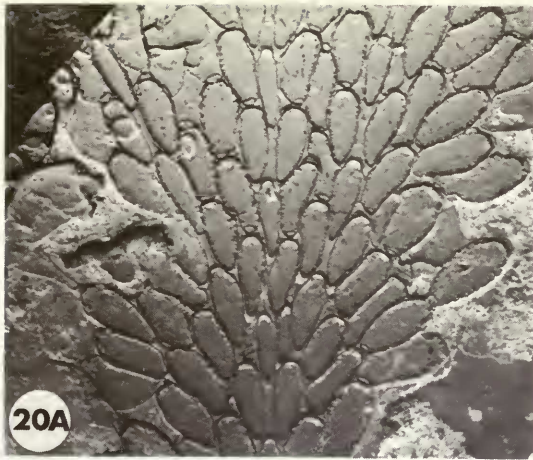
Spinicharixa dimorpha sp. nov.

Figs 20–27

?1892 *Membranipora fragilis* d'Orbigny var?; Vine: 155.

HOLOTYPE. BMNH D53152a. Cristatum Nodule Bed, U. Gault Clay, U. Albian (*inflatum* Zone, *cristatum* Subzone). Naccolt Brickworks, Wye, Ashford, Kent. A. Gale Colln. Preserved as a mould on the surface of a phosphatic steinkern.

PARATYPES. BMNH D53152b, c, on the same substrate as the holotype. D35361, Gault Clay, Dunton Green, Sevenoaks, Kent, D. Forbes Colln (probably from the M.–U. Albian *lautus* Zone nodule bed; H. G. Owen personal communication, 1984). D46898, Gault Clay Bed 9, U. Albian (*inflatum* Zone, *orbigny* Subzone), Greatness Lane, Sevenoaks, Kent, J. S. H. Collins Colln. These four specimens are, like the holotype, preserved as moulds on the surface of phosphatic steinkerns. D55066 (several broken colonies), L. Gault Clay, M. Albian (*loricatus* Zone, *intermedius* Subzone), Copt Point, Folkestone, Kent, A. Gale & D. Horne Colln.



Figs 20–21 *Spinicharixa dimorpha* gen. et sp. nov.; Gault Clay (Albian); phosphatic moulds of colony undersides. Fig. 20, BMNH D53152a, **holotype**; Naccolt Brickworks, Ashford, Kent; 20A, caudate and non-caudate autozooezia, $\times 14$; 20B, newly-budded non-caudate autozooezium with well-defined pore chambers, $\times 65$; 20C, same autozooezium showing large distal and smaller distolateral pore chambers, $\times 137$. Fig. 21, BMNH D35361, **paratype**; Dunton Green, Sevenoaks, Kent; distal part of the closure plate of a caudate autozooezium showing lunate impressions of the opercular sclerites, $\times 330$.

NAME. In reference to the two types of autozooezia.

DESCRIPTION. Colonies are encrusting and pluriserial (Fig. 20a). The budding pattern is very distinctive (Fig. 22); lines of long, narrow, caudate autozooezia bud distolateral autozooezia which are short, broad and non-caudate and are orientated subparallel to their parent autozooezium. These non-caudate autozooezia bud further non-caudate autozooezia distally and distolaterally to infill the space between the lineal series of caudate autozooezia. Irregular interzooezial gaps are often left and the autozooezia are less tightly packed than in *S. pittii*. Non-caudate autozooezia occasionally give rise to new lineal series of caudate zooezia, originating as distal buds and generally separated from earlier series of caudate autozooezia by two generations of non-caudate autozooezia.

Autozooezia are large, caudate autozooezia averaging 1.35 mm long by 0.26 mm wide and having a pyriform outline, whereas non-caudate autozooezia average 0.92 mm long by 0.36 mm

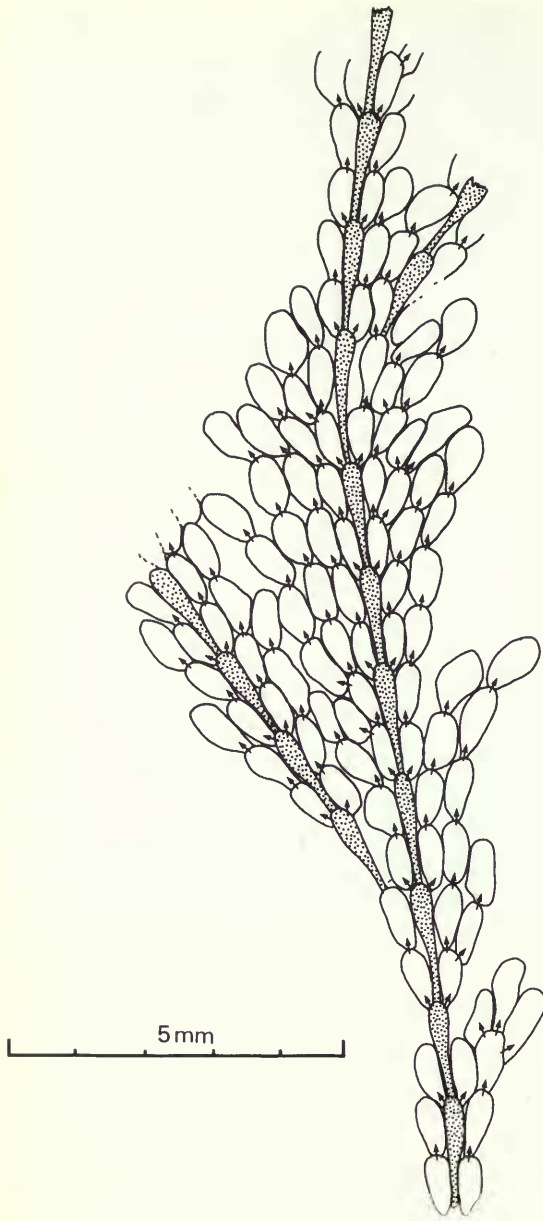


Fig. 22 *Spinicharixa dimorpha* gen. et sp. nov. Outline diagram of paratype BMNH D35361 to show budding pattern. Caudate autozooezia are stippled; arrows indicate budding directions.

wide and are subelliptical in outline. Opesia are extensive in both types of autozooezia. Gymnocysts are narrow except in caudate zooezia in which the proximal gymnocyst is elongate. Cryptocysts are also narrow and are steeply sloping, pustulose, and have crenulate boundaries with the gymnocysts. Small, circular to elliptical spine bases occur in variable numbers (Fig. 25b). Caudate autozooezia may have up to eight pairs of spine bases, but non-caudate autozooezia, especially those distant from caudate series, have fewer, apparently sometimes restricted to a distal pair. The spine bases are often located within the gymnocystal furrows between the opesia of adjacent autozooezia (Fig. 25a). In contrast to *S. pitti*, they rarely indent the outer edge of the cryptocyst. However, like *S. pitti*, well-preserved spine bases have an inner concentric ring resembling that found in the Recent anascan *Callopora lineata*.

Pore chambers are conspicuous only in newly budded autozooezia, in which a large distal pore chamber occurs together with up to three pairs of smaller pore chambers situated distolaterally, laterally or proximolaterally (Fig. 20b, c). Ontogenetically older autozooezia proximal of the growing edge appear to lose their pore chambers. Ontogenetic series of the large distal pore chambers seem to show a progressive resorption of the distal exterior wall of the pore chamber occurring concurrently with thickening of the proximal interior wall (Figs 23, 24). This eliminates the pore chamber in older zooezia and sometimes appears to sever continuity between zooezia *via* communication pores. However, the phosphatic infill of the chambers of some proximal–distal pairs of autozooezia are linked by a thread which may represent the cast of a communication pore (Fig. 23c, d).

Regenerated mural rims are uncommon and have been observed only in non-caudate autozooezia. Some of the caudate autozooezia are occluded by smooth convex closure plates (Fig.

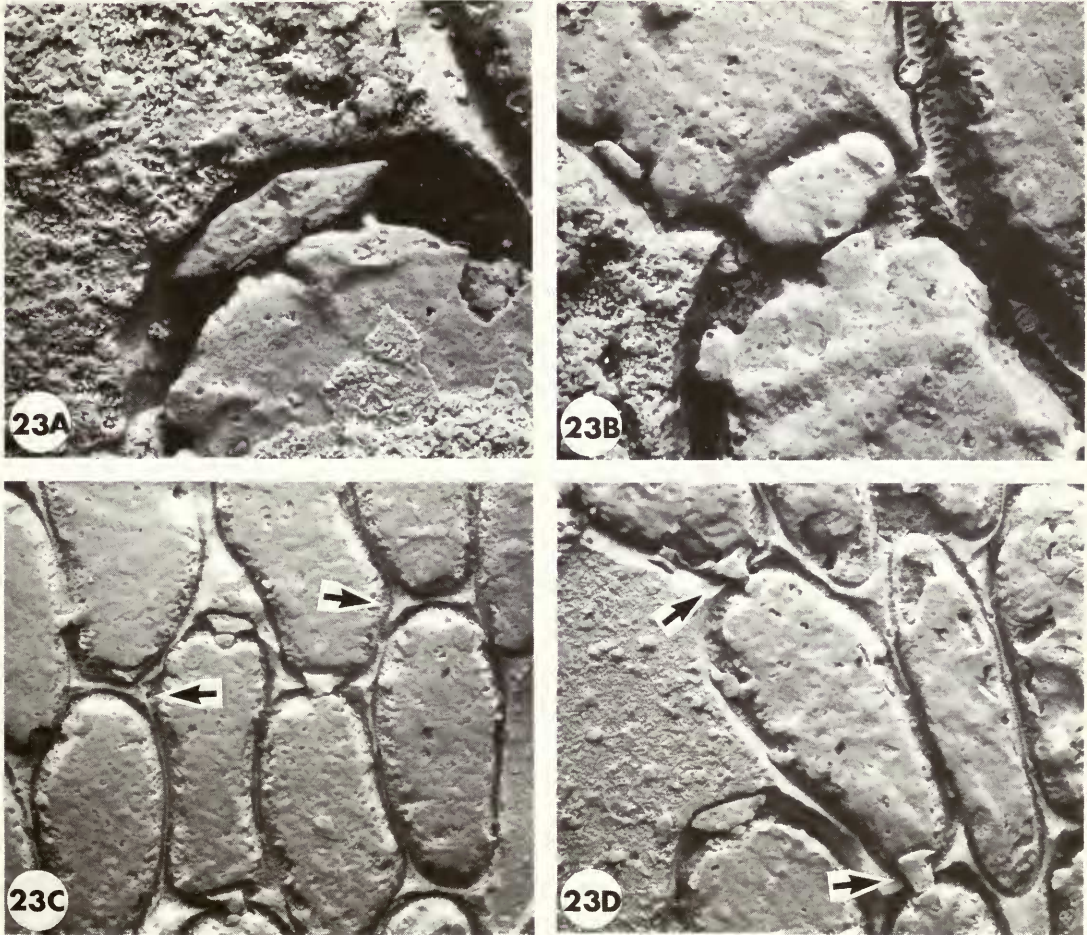


Fig. 23 *Spinicharixa dimorpha* gen. et sp. nov.; BMNH D35361, paratype; Gault Clay (Albian); Dunton Green, Sevenoaks, Kent; phosphatic moulds of undersides of zooezia with pore chambers; 23A, well-defined distal pore chamber in an autozooezium slightly more advanced in ontogeny than that depicted in Fig. 20B, $\times 190$; 23B, distal pore chamber with an ill-defined distal exterior wall in an autozooezium still more advanced, $\times 190$; 23C, autozooezia apparently lacking pore chambers in their distal transverse walls (arrows), together with others in which the distal pore chambers are still visible, $\times 48$; 23D, autozooezia linked by phosphatic threads (arrows) suggesting open interzooidal pores between zooezia in proximal–distal series, $\times 64$.

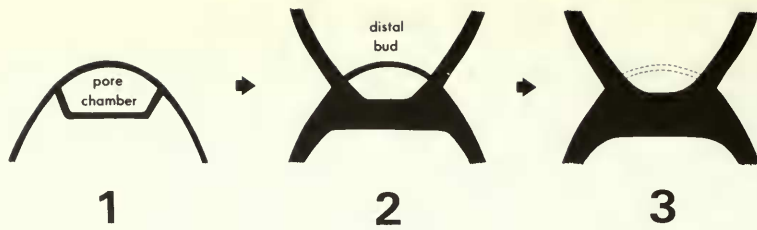
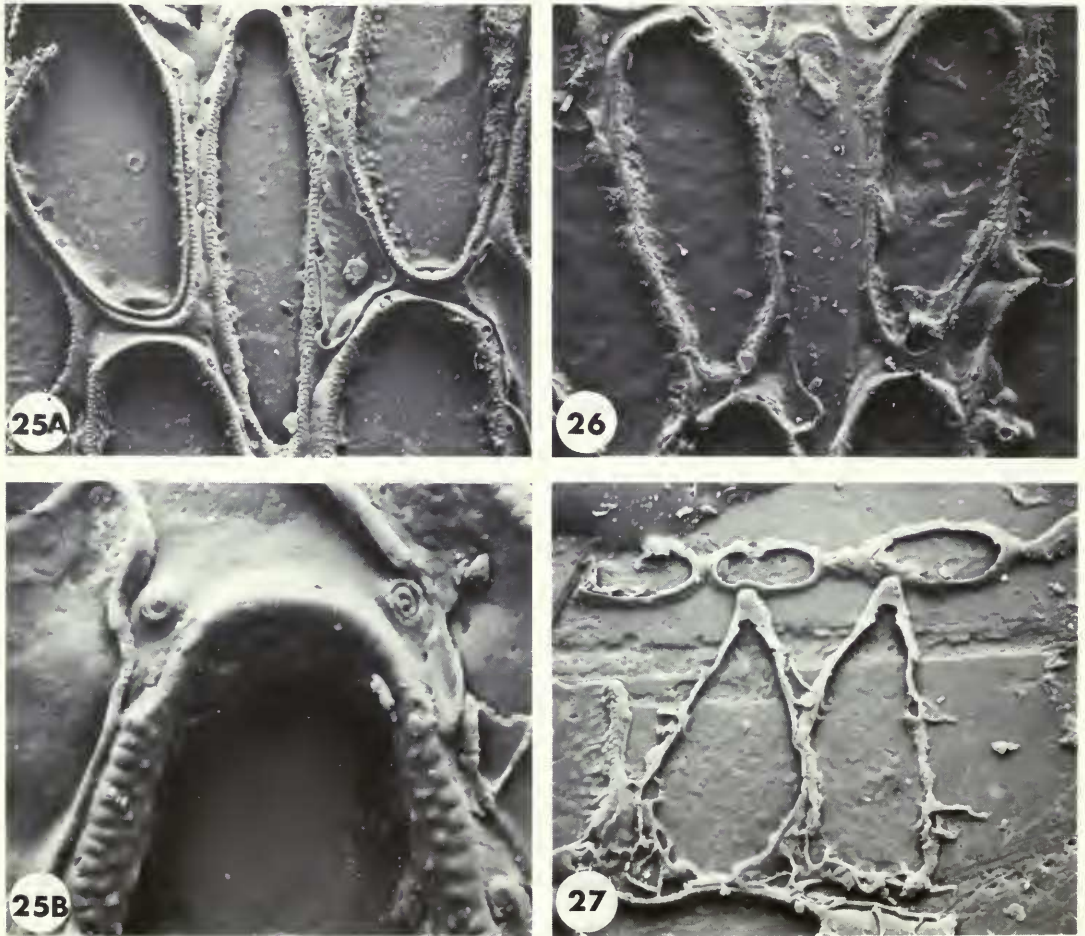


Fig. 24 Diagram of the apparent ontogeny of a distal pore chamber in *Spinicharixa dimorpha* gen. et sp. nov. Sequence inferred from phosphatic moulds in which only the basal outlines of the structures are generally visible; any interzooidal pores located above basal level are not visible in the sequence shown. Initially (Stage 1), the curved exterior wall of the pore chamber and the interior wall (septulum) are thin. Concurrently with the budding of a distal zooid from the pore chamber (Stage 2), all walls are thickened by calcification except for the curved length of exterior wall which is now enclosed by the newly budded zooid. Finally (Stage 3), this curved length of exterior wall is resorbed so that the two zooecia in lineal series are separated only by the thickened septulum.



Figs 25–27 *Spinicharixa dimorpha* gen. et sp. nov.; Gault Clay (Albian); latex casts prepared from phosphatic moulds. Fig. 25, BMNH D53152a, holotype; Naccolt Brickworks, Ashford, Kent; 25A, elongate opesiae of a caudate autozoocium, $\times 82$; 25B, distal spine bases of a caudate autozoocium, $\times 370$. Fig. 26, BMNH D35361, paratype; Dunton Green, Sevenoaks, Kent; caudate autozoocium with a closure plate, $\times 66$. Fig. 27, BMNH D53152b, paratype; apparent bipolar pair (top) of astogenetically early autozoocia each budding a large, incompletely formed autozoocium orientated at right angles, $\times 70$.

26) which occasionally bear a pair of crescentic impressions, about 0.10 mm apart, left by the opercular sclerites (Fig. 21). Closure plates have not been observed in non-caudate autozoecia.

Early astogenetic autozoecia are preserved in colony D53152b, in which the colony origin can be traced to two small autozoecia joined proximally and growing in opposite directions (Fig. 27). One is about 0.24 mm long, the other 0.33 mm long. The smaller of the two has a slight V-shaped notch in its proximal gymnocyst from which the larger autozoecium appears to emerge. This structure suggests fracturing of the proximal part of the smaller autozoecium to produce the V-shaped notch, followed by regenerative growth of an oppositely orientated bud from the fracture to give a 'bipolar pair' of zooecia (Taylor 1986). Although it is conceivable that the smaller of the two autozoecia is the ancestrula, the ancestrula and other astogenetically earlier autozoecia may have been removed during fracturing. Each of the two autozoecia have small distal buds and much larger lateral or distolateral buds orientated at right angles to their parent autozoecia (Fig. 27). A poorly-preserved but apparently similar bipolar pair is present in D55066, involving autozoecia of an astogenetically 'mature' size.

Kenozoecia (Figs 25a, 26) occupy some of the irregular spaces between autozoecia and overlap slightly onto the gymnocysts of the autozoecia. They are polygonal in outline, open and relatively featureless, seeming to lack cryptocyst, significant gymnocyst and spine bases.

Ovicells and avicularia are absent.

REMARKS. *S. dimorpha* is readily distinguished from previously described species by the dimorphism of the autozoecia and the characteristic growth pattern in which non-caudate autozoecia fill in the areas between linear series of caudate autozoecia. The growth is similar to that found in some colonies of Recent species of *Electra* and *Conopeum*. Suboptimal diet has been shown to produce this growth pattern in colonies of *C. tenuissimum*, whereas well-fed colonies grow in compact sheets (Winston 1976). However, the growth pattern is species-characteristic in *Electra* and not ecophenotypic.

Table 1 Zooecial dimensions (mm) determined from a minimum of ten autozoecia for each of seven species of *Charixa* and *Spinicharixa*.

	zl	zw	ol	ow		zl	zw
<i>C. vennensis</i> (p. 201)					<i>S. pitti</i> (p. 210)		
\bar{x}	0.51	0.24	0.24	0.14	\bar{x}	0.41	0.25
SD	0.134	0.043	0.038	0.024	SD	0.027	0.037
r	0.21-0.66	0.18-0.32	0.17-0.27	0.11-0.18	r	0.36-0.45	0.20-0.35
<i>C. lhuydi</i> (p. 203)					<i>S. dimorpha</i> : non-caudate (p. 215)		
\bar{x}	0.44	0.33	0.31	0.22	\bar{x}	0.92	0.36
SD	0.039	0.032	0.039	0.023	SD	0.099	0.036
r	0.38-0.50	0.30-0.39	0.24-0.36	0.18-0.26	r	0.80-1.11	0.29-0.41
<i>C. cryptocauda</i> (p. 205)					<i>S. dimorpha</i> : caudate (p. 215)		
\bar{x}	0.53	0.24	0.33	0.16	\bar{x}	1.35	0.26
SD	0.056	0.039	0.029	0.027	SD	0.096	0.019
r	0.44-0.62	0.18-0.32	0.29-0.39	0.12-0.21	r	1.16-1.50	0.21-0.29
<i>C. lindiensis</i> (p. 208)					Abbreviations: zl, zooecial length; zw, zooecial width; ol, opesial length; ow, opesial width; \bar{x} , mean; SD, standard deviation; r, observed range.		
\bar{x}	0.41	0.20	0.27	0.13			
SD	0.034	0.023	0.033	0.017			
r	0.36-0.45	0.17-0.24	0.21-0.32	0.11-0.17			
<i>C.?</i> sp. (p. 208)							
\bar{x}	0.72	0.34	0.42	0.21			
SD	0.057	0.045	0.052	0.040			
r	0.66-0.84	0.30-0.45	0.32-0.48	0.15-0.27			

There are sufficient differences between *S. dimorpha* and the type species of *Spinicharixa*, *S. pittii*, to suggest that assignment to a separate genus may be appropriate when more is known of primitive anascans.

DISTRIBUTION. M. Albian (*loricatus* Zone, *intermedius* Subzone)—U. Albian (*inflatum* Zone, *orbigny* Subzone) Gault Clay of Kent, England.

Discussion

The established stratigraphical range of cheilostome bryozoans extends from the Upper Jurassic to the Recent. During approximately the first third of their history, until the late Albian, cheilostomes remained morphologically simple and conservative, and were taxonomically depauperate. They were uncommon in terms of numerical abundance, despite attaining a widespread geographical distribution with a broad palaeolatitudinal range.

The majority of pre-late Albian cheilostomes had uniserial, pluriserial or loosely-organized multiserial colonies in which interzooidal communication between zooidal series was lacking or very restricted. The Polish Valanginian–Hauterivian species *Wawalia crenulata* is an exception in having tightly-packed zoecia forming multiserial colonies in which regular communication pores apparently linked zooids in adjacent series (Dzik 1975: fig. 3a). All early Cretaceous species known from adequately preserved material appear to have pore chambers; failure to record pore chambers in some species may be owing to poor preservation and perhaps also to their resorption in ontogenetically older zooids (cf. *Spinicharixa dimorpha*, p. 217). Budding was intrazooidal (*sensu* Lidgard 1985). Opesiae are extensive and bordered by steeply sloping cryptocysts which are little more than outwardly flared continuations of vertical walls. Cryptocysts are ornamented by pustules (e.g. *Spinicharixa*), radial striae (*Pyriporopsis*) or striae which break into pustules towards the centre of the zooid (*Wawalia*). The boundary between the cryptocyst and the surrounding gymnocyst is ill-defined, crenulated and does not involve a significant change in vertical relief (cf. *Wilbertopora* where the outer edge of the cryptocyst is raised above the level of the gymnocyst). Proximal gymnocysts are moderately to well developed, especially in uniserial species which may have distinctly caudate zooids. Spine bases occur regularly in some species (*Spinicharixa* spp.) and sporadically in others (e.g. *Charixa lindiensis*, *Pyripora texana*). Regular spine bases can be large and may indent the margin between gymnocyst and cryptocyst, whereas sporadic spine bases are small, paired and distally situated ('orificial'). Kenozoecia may be found in most or all species and apparently represent zooids budded into irregular and restricted spaces. Unequivocal ovicells and avicularia have not been described in pre-late Albian cheilostomes.

A significantly more advanced morphological grade first appears in the late Albian species *Wilbertopora mutabilis* from the U.S.A. (Cheetham 1954, 1975), together with a few poorly described species (e.g. '*Membranipora*' *elliptica* (?) Hagenow of Vine, 1890a) from the contemporaneous Red Chalk of Britain, which have ovicells and avicularia. The great majority of anascans involved in the late Cretaceous radiation of the Cheilostomata were also species with ovicells and avicularia. The attainment of this grade of organization may have considerable relevance to the diversification of cheilostomes during the late Cretaceous.

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References

- Aguilar, M. J., Ramirez del Pozo, J. & Riba, O. 1971. Algunas precisiones sobre la sedimentación y paleoecología del Cretácico inferior en la Zona Utrillas-Villarroya de los Pinares (Teruel). *Estudios geol. Inst. Invest. geol. Lucas Mallada*, Madrid, 27: 497–512.
- Banta, W. C. 1975. Origin and early evolution of cheilostome Bryozoa. *Docums Lab. Géol. Fac. Sci. Lyon*, (H.S.) 3: 565–582.

- Boardman, R. S. et al.** 1983. Bryozoa. In Robison, R. A. (ed.), *Treatise on Invertebrate Paleontology*, G (1). 625 pp., 295 figs. Lawrence, Kansas.
- Canu, F. & Bassler, R. S.** 1926. Studies on the cyclostomatous Bryozoa. Part 2. Lower Cretaceous cyclostomatous Bryozoa. *Proc. U.S. natn. Mus.*, Washington, **67** (21): 1–160.
- Cheetham, A. H.** 1954. A new early Cretaceous cheilostome bryozoan from Texas. *J. Paleont.*, Tulsa, **28**: 177–184.
- 1975. Taxonomic significance of autozooid size and shape in some early multiserial cheilostomes from the Gulf Coast of the USA. *Docums Lab. Géol. Fac. Sci. Lyon*, (H.S.) **3**: 547–564.
- Cleavelly, R. J., Morris, N. J. & Bate, G.** 1984. An ecological consideration and comparison of the Punfield Marine Band (Lower Aptian) Mollusca. *Proc. Dorset nat. Hist. archaeol. Soc.*, Dorchester, **105**: 93–106.
- Dzik, J.** 1975. The origin and early phylogeny of the cheilostomatous Bryozoa. *Acta paleont. pol.*, Warsaw, **20**: 395–423.
- Ensom, P. C.** 1985. *Pyripopsis portlandensis* Pohowsky 1973, a bryozoan from the Scallop Member, Purbeck Limestone Formation, of Worbarrow Tout, Dorset. *Proc. Dorset nat. Hist. archaeol. Soc.*, Dorchester, **106**: 167.
- Etheridge, R. jr** 1901. Additional notes on the palaeontology of Queensland (Part 2). *Bull. geol. Surv. Qd*, Brisbane, **13**: 1–37.
- 1902. A monograph of the Cretaceous invertebrate fauna of New South Wales. *Mem. geol. Surv. N.S.W.*, Sydney, (Palaeont. ser.) **11**: 1–98.
- Hayward, P. J. & Cook, P. L.** 1983. The South African Museum's *Meiring Naude* cruises. Part 13. Bryozoa II. *Ann. S. Afr. Mus.*, Cape Town, **91** (1): 1–161.
- Kennedy, W. J. & Klinger, H. C.** 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **25** (4): 263–315.
- Lang, W. D.** 1915. On some new uniserial Cretaceous cheilostome Polyzoa. *Geol. Mag.*, London, (6) **2**: 496–504.
- Larwood, G. P.** 1973. New species of *Pyripora* d'Orbigny from the Cretaceous and the Miocene. In Larwood, G. P. (ed.), *Living and Fossil Bryozoa*: 463–473. London.
- 1975. Preliminary report on early (pre-Cenomanian) cheilostome Bryozoa. *Docums Lab. Géol. Fac. Sci. Lyon*, (H.S.) **3**: 539–545.
- 1979. Colonial integration in Cretaceous cribrimorph Bryozoa. In Larwood, G. P. & Abbott, M. B. (eds), *Advances in Bryozoology*: 503–520. London.
- & Taylor, P. D. 1981. Mesozoic bryozoan evolution: response to increasing predation pressure? In Larwood, G. P. & Nielsen, C. (eds), *Recent and Fossil Bryozoa*: 312–313. Fredensborg.
- Lidgard, S.** 1985. Zooid and colony growth in encrusting cheilostome bryozoans. *Palaeontology*, London, **28**: 255–291.
- Mantell, G. A.** 1844–54. *The Medals of Creation*, 1. 1st edn. 456 pp. (1844). 2nd edn. 446 pp. (1854). London.
- Masse, J. P. & Walter, B.** 1974. Les Bryozoaires du Crétacé Inférieur Provençal. Biostratigraphie et Paléoécologie. *Géobios*, Lyon, **7**: 183–210.
- Mortensen, T.** 1928. *A monograph of the Echinoidea*, 1. Cidaroidea. 551 pp. Copenhagen.
- Orbigny, A. d'** 1851–54. *Paléontologie française. Terrains crétacés*, 5. Bryozoaires. 1191 pp. Paris.
- Pitt, L. J.** 1976. A new cheilostome bryozoan from the British Aptian. *Proc. Geol. Ass.*, London, **87**: 65–68.
- Pohowsky, R. A.** 1973. A Jurassic cheilostome from England. In Larwood, G. P. (ed.), *Living and Fossil Bryozoa*: 447–461. London.
- 1978. The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bull. Am. Paleont.*, Ithaca, **73** (301): 1–192.
- Ryland, J. S. & Hayward, P. J.** 1977. *British anascan bryozoans*. 188 pp. London (Synopses Br. Fauna, n.s. 10).
- Schopf, T. J. M.** 1977. Patterns and themes of evolution among the Bryozoa. In Hallam, A. (ed.), *Patterns of Evolution*: 159–207. Amsterdam.
- Scott, R. W.** 1970. Paleocology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas. *Paleont. Contr. Univ. Kansas*, Lawrence, Art. **52**: 1–94.
- Silén, L.** 1942. Origin and development of the cheilo-ctenostomatous stem of Bryozoa. *Zool. Bidr. Upps.*, **22**: 1–59.
- Taylor, P. D.** 1981a. Functional morphology and evolutionary significance of differing modes of tentacle eversion in marine bryozoans. In Larwood, G. P. & Nielsen, C. (eds), *Recent and Fossil Bryozoa*: 235–247. Fredensborg.
- 1981b. Bryozoa from the Jurassic Portland Beds of England. *Palaeontology*, London, **24**: 863–875.

- 1986. The ancestrula and early growth pattern in two primitive cheilostome bryozoans: *Pyripora catenularia* (Fleming) and *Pyriporopsis portlandensis* Pohowsky. *J. nat. Hist.*, London, **20**: 101–110.
- Thomas, H. D. & Larwood, G. P.** 1956. Some 'uniserial' membraniporine polyzoan genera and a new American Albian species. *Geol. Mag.*, Hertford, **93**: 369–376.
- 1960. The Cretaceous species of *Pyripora* d'Orbigny and *Rhammatopora* Lang. *Palaeontology*, London, **3**: 370–386.
- Vine, G. R.** 1890a. The Polyzoa of the Red Chalk of Hunstanton. *Q. Jl geol. Soc. Lond.*, **46**: 454–486.
- 1890b. Notes on the Polyzoa and Microzoa of the Red Chalk of Yorkshire and Norfolk. *Proc. Yorks. geol. polytech. Soc.*, Leeds, **11**: 363–396.
- 1892. Fossil Polyzoa: further additions to the Cretaceous lists. *Proc. Yorks. geol. polytech. Soc.*, Leeds, **12**: 149–161.
- Voigt, E.** 1968. On the Cretaceous age of the so-called Jurassic cheilostomatous Polyzoa (Bryozoa). *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **17**: 1–45.
- 1980. *Arachnidium longicauda* n. sp. (Bryozoa Ctenostomata) aus der Maastrichter Tuffkreide (Ob. Kreide, Maastrichtium). *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **1980**: 738–746.
- 1981. Répartition et Utilisation Stratigraphique des Bryozoaires du Crétacé Moyen (Aptien-Coniacien). *Cret. Res.*, London, **2**: 439–462.
- Wilson, V., Welch, F. B. A., Robbie, J. A. & Green, G. W.** 1958. Geology of the Country around Bridport and Yeovil. *Mem. geol. Surv. Gt Br.*, London, sheets **327 + 312**. 239 pp.
- Winston, J. E.** 1976. Experimental culture of the estuarine ectoproct *Conopeum tenuissimum* from Chesapeake Bay. *Biol. Bull. mar. biol. Lab. Woods Hole*, **150**: 318–335.